Mobility of Mass-Reared Diapaused and Nondiapaused *Cydia pomonella* (Lepidoptera: Tortricidae): Effect of Different Constant Temperatures and Lengths of Cold Storage

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ABSTRACT Desirable behavioral attributes in mass-reared insects should include the ability to perform favorably under the various environmental conditions they encounter upon release in the field. Insect quality also may be influenced by storage conditions and storage duration before field release. We studied the effects of three different constant ambient temperatures (15, 20, and 25°C) and different lengths of adult cold storage (0, 24, 48, and 72 h at 2°C) on the locomotor activity of adult *Cydia pomonella* (L.) mass reared through diapause or standard production protocols. Mobility was assessed in actographs housed in a climate controlled chamber; tests lasted 24 h. We found that adult mobility was significantly higher for both males and females at 25 and 20°C than at 15°C. There were no significant differences in mobility in moths reared through diapause or nondiapaused production protocols. In addition, temporal analysis of the data revealed a significant shift in the diel patterns of activity for both genders when adults were tested at the three different temperatures. Moths exposed to the lower temperature shifted their activity pattern from evening to mid-afternoon, which may be an adaptive behavior to take advantage of the expected warmest period of the day. Diapaused adults were significantly less mobile when stored in the cold (24, 48, or 72 h of storage at 2°C) than were diapaused adults that did not experience cold storage (0 h). However, length of time in cold storage did not significantly influence the mobility of adult codling moths reared through standard production protocols.

KEY WORDS codling moth, quality control, locomotor activity, temperature

Measurements of insect quality in colonies that are destined for use in pest management programs should include the evaluation of key behavioral and life history traits (Gandolfi et al. 2003, Calkins and Parker 2005). Desirable behavioral attributes are intimately linked to how well a mass-reared insect population functions in its intended role, that is, how effectively it interacts with and impacts upon the target population (Huettel 1976). Laboratory bioassays have been developed to quantify different behavioral parameters in laboratory colonies (Cayol et al. 1999, Dorn et al. 1999, Lux 1999) and to examine insect behavioral responses under different simulated environmental conditions (Lance et al. 1988, Todd et al. 2002). Maintaining or improving the quality of mass-reared laboratory-adapted insects is essential if programs using the sterile insect technique (SIT) are to be successful (Calkins and Ashley 1989).

The SIT, as currently implemented by the Okanagan-Kootenay Sterile Insect Release (OKSIR) Program in British Columbia, Canada, relies on insects that are mass reared, treated with gamma radiation, and released for areawide control of the codling moth, *Cydia pomonella* (L.). Larvae are reared on agar-free diet (Brinton et al. 1969) at 27°C and adults (rather than pupae) are collected as they emerge from the diet. UV lights attract the adults to ducts that transport them to a cold room (2°C) where they are immobilized. Inside the cold room, insects are packaged into petri dishes and treated with 250 Gy of gamma radiation within 1–20 h after collection. Irradiated adults are kept in the cold room until taken to the field in refrigerated vehicles or in electric coolers affixed to ground-release vehicles. Eighty to ninety percent of the moths are released into area orchards within 24–36 h of adult collection. However, when adverse environmental conditions occur, moths can be stored at 2°C for up to 72 h before field release. Additional details on codling moth mass rearing can be found in Bloem et al. (2000).

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Codling moths reared at constant high temperature are less active in the spring compared with wild moths that have overwintered as mature fifth instars in the orchard (Proverbs 1971). In an attempt to address this problem and to increase the production efficiency of the OKSIR Program, Bloem et al. (1997, 2000) developed techniques to mass rear codling moths through diapause. Later, field performance of mass-reared diapaused and nondiapaused (standard production) moths was evaluated after treatment with different doses of gamma radiation: 330 Gy (Bloem et al. 1998) and 250 and 150 Gy (Bloem et al. 2004). These studies revealed that recapture of diapaused moths was significantly higher than recapture of moths reared through standard production irrespective of time of the year when experiments were conducted. However, the effect that different ambient temperatures may have on field performance of diapaused and nondiapaused unirradiated codling moths has not been evaluated. Furthermore, although minimizing the length of adult cold storage may be important in preserving the quality of irradiated codling moths destined for field release (Bloem and Bloem 2000), supporting data on the effect of the length of cold storage on adult mobility are not yet available.

Codling moth locomotor activity has been characterized in several laboratory studies by using actographs. For example, mobility was measured in groups of mixed sex laboratory-adapted moths at 26°C by Boving et al. (1978) or in single gender cohorts at 22°C by Keil et al. (2001a), individuals with high and low mobility were identified for use in bidirectional selection by Keil et al. (2001b), and sublethal effects of pesticides and hormone mimics were investigated by Dorn and Gu (1999) and Keil et al. (2001a). In addition, patterns of adult activity in four tortricid orchard pests (including codling moth) by using both timed traps and ultrasonic actographs were studied by Knight et al. (1994). Diel rhythms of mobility in laboratory-reared moths have been correlated with field observations of circadian rhythm and have been used to evaluate not only the quality of laboratory colonies but whether their performance, and the data generated by the laboratory device accurately reflects field reality (Schumacher et al. 1997a, Hughes and Dorn 2002). Diel rhythms of mobility at different constant temperatures have been documented for the corn earworm, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), by Hsiao (1978). However, no comparative effect of different constant ambient temperatures on diel patterns of locomotor activity has been reported for *C. pomonella.*

In the current study, we used computer-linked infrared actographs to examine the effect of different constant temperatures on the mobility of adult codling moths, *C. pomonella*, mass-reared through diapause or standard production protocols. We also studied the effect of length of adult cold storage on adult mobility. In a companion article (Bloem et al. 2006), we examined the mobility of diapaused and nondiapaused moths and the effect of mating status and treatment with different doses of gamma radiation. The results of these evaluations are presented herein, and the importance of the data to the implementation of a successful areawide sterile insect release program for *C. pomonella* is discussed.

Materials and Methods

Test Insects. The codling moth colony at the OKSIR mass-rearing facility has been in continuous culture since 1993 (≈10 generations per year), but its genetic stock is refreshed through the introduction of 50–100% feral males in the winter of most years. Two mass-rearing strategies (standard [N] and diapause [D]) were used to prepare the insects for our experiments. Detailed procedures on insect preparation can be found in Bloem et al. (2006). Insects were reared in Canada and experiments were conducted in Switzerland during 2005.

Standard and diapause-reared pupae were sorted by gender, placed in plastic petri dishes (9 cm in diameter), and kept at 27°C, 70% RH, and a photoperiod of 16:8 (L:D) h until shipment to Switzerland. A section of moistened cotton wool was placed in each petri dish before packaging the dishes into small insulated boxes. An electronic data pod (Hobo, Onset, Bourne, MA) was included to record temperature during transport. Insects were shipped via courier to the Institute of Plant Sciences/Applied Entomology, Swiss Federal Institute of Technology (ETH), Zurich, Switzerland. Upon arrival, pupae of each rearing strategy and gender were placed in separate plastic emergence cages (21 by 21 by 17 cm) and kept at 26°C, 65% RH, and a photoperiod of 16:8 (L:D) h.

Effect of Constant Temperature on Locomotor Activity. Emerging adults were collected once per day, placed individually in glass vials (28 by 80 mm), and given access to moisture. Insects were held at 26°C, 65% RH, and a photoperiod of 16:8 (L:D) h for 24 h before testing. Experiments were conducted in February 2005 by using 30 infrared actographs (Activity Monitor, Electronic Services Unit, University of New England, Armidale, New South Wales, Australia) located inside a walk-in climate controlled chamber (Conviron, model PGV 36, Controlled Environments Limited, Winnipeg, Manitoba, Canada). Each actograph is composed of a transmitter that emits an infrared light beam that is captured by a receiver/logic-converter linked to a computer. Individual test insects inside closed glass vials (28 by 80 mm) are positioned between the transmitter and the receiver. Any movement that intercepts the infrared beam triggers a signal that is recorded by the computer. *C. pomonella* adults intercepted the infrared beam nearly exclusively by flight (S.B., unpublished data). Because artificially elevated counts can occur when an insect flutters in the path of the infrared beam, recorded signals that occurred more than twice within the same second of time were eliminated by application of a specific analytical program (M. Gernss, ETH). Thus, a mobility count is defined as an interception of the infrared beam excluding this artifact.

Cohorts of 24–48-h-old virgin adults from each rearing strategy (N and D) were tested one gender at a time. Treatment temperatures were 25, 20, and 15°C, and all tests lasted 24 h. Relative humidity (60%) and photoperiod were the same for all treatments. Insects were brought into the climate-controlled chamber and allowed to acclimate to the treatment temperature for a minimum of 1 h before initiating the test. Test insects were placed in the actographs at random, and experiments were initiated 2 h before the onset of dusk. Light intensity was 3,750 lux at photophase (16 h) and 0.1 lux at scotophase (4 h). Between these two phases, there were simulated dusk and dawn periods lasting 2 h each, during which illumination was gradually decreased or increased between 3,750 and 0.1 lux in 10-min steps. In total, 25–45 individuals of each rearing strategy and gender (N males, D males, N females, and D females) were tested at each treatment temperature (25, 20, and 15°C).

Effect of Length of Time in Cold Storage on Adult Locomotor Activity. As mentioned above, emerging adults from each rearing strategy were collected once per day and placed in glass vials (28 by 80 mm) with access to moisture. Insect treatments were 0 h of cold storage (=control) or 24, 48, or 72 h of storage at 2°C, 85% RH, and a photoperiod 0:24 (L:D) h. Tests for locomotor activity lasted for 24 h, and genders were tested separately. A minimum of 15–18 individuals from each treatment, rearing strategy, and gender were tested. Experiments were conducted during March 2005 by using the actograph equipment and the procedures described above. Insects were allowed to acclimate inside the chamber for 1 h before testing. The actograph chamber was maintained at 25°C, 60% RH, and a photoperiod of 16:8 (L:D) h for the duration of the study.

Data Analysis. *Effect of Constant Temperature on Locomotor Activity.* Mobility counts were $\log_{10}$ transformed to stabilize their variance, and the data were analyzed using multifactor analysis of variance (ANOVA) with treatment temperature (25, 20, or 15°C), type of rearing strategy (D or N), and insect gender (M or F) as sources of variation (PROC GLM) (SAS Institute 1989). All interactions were included in the statistical model. When significant differences were detected, means were separated by the Tukey–Kramer statistic at $P = 0.05$ (SAS Institute 1989).

In a follow-up analysis, corrected mobility counts were summed for intervals of 15 min. Cumulative counts as well as cumulative $\log_{10}$-transformed counts were calculated for each 24-h period. Data were analyzed using multifactor ANOVA with temperature (25, 20, or 15°C), type of rearing strategy (D or N), insect gender (M or F), test day, and time interval as sources of variation (PROC GLM) (SAS Institute 1989). All interactions, including sixth order polynomials for time interval, were included in the statistical model. Because there was a three-way interaction between temperature, gender, and time interval, data also were sorted by gender and temperature and subjected to sixth order polynomial regression analysis to examine the relationship between time interval and the cumulative $\log_{10}$-transformed mobility counts (PROC GLM) (SAS Institute 1989).

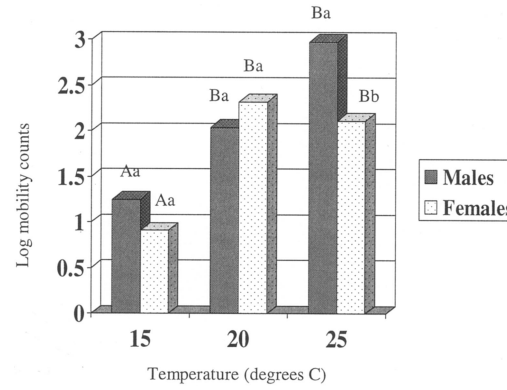

Fig. 1. Effect of three different constant temperatures (15, 20, and 25°C) on the locomotor activity of 24–48-h-old adult *C. pomonella* as measured in infrared actographs. Mobility counts were $\log_{10}$ transformed to stabilize the variance. Uppercase letters compare means between treatments within one gender. Lowercase letters compare means between genders within each temperature.

Effect of Length of Time in Cold Storage on Adult Locomotor Activity. Mobility counts were analyzed using multi-factor ANOVA with length of time in cold storage (0, 24, 48, or 72 h), type of rearing strategy (D or N), and insect gender (M or F) as sources of variation (PROC GLM) (SAS Institute 1989). All interactions were included in the statistical model. When significant differences were indicated, means were separated by the Tukey–Kramer statistic at $P = 0.05$ (SAS Institute 1989).

Results

Effect of Constant Temperature on Locomotor Activity. The mobility of 24–48-h-old mass-reared codling moths was significantly influenced by an interaction between treatment temperature (25, 20, or 15°C) and insect gender (M or F) ($F = 12.87$; df = 2, 346; $P < 0.0001$) (Fig. 1). Adult mobility was significantly higher for both male and female codling moths at treatment temperatures of 25 and 20°C than at a temperature of 15°C. The locomotor activity of male and female codling moths was similar at 20 and at 15°C; however, male mobility was significantly higher than female mobility at 25°C. No significant differences were detected in mobility at the different constant temperatures due to rearing strategy.

When data were further analyzed by 15-min time intervals, we discovered that mobility (cumulative $\log_{10}$-transformed counts) for male and female codling moths was significantly influenced by a three-way interaction between temperature (25, 20, or 15°C), gender (M or F), and time interval ($F = 7.35$; df = 2, 29263; $P < 0.0006$). Polynomial regression analyses revealed significant relationships between time interval and the cumulative $\log_{10}$-transformed mobility counts for both male and female adults at each con-

Table 1. Polynomial relationships between time interval and the cumulative $\log_{10}$-transformed mobility counts for 24–48-h-old adult *C. pomonella* at different constant temperatures (15, 20, and 25°C)

Gender	Temp (°C)	Regression equation	*F*	*P*
Male	15	$y = -0.123 + 0.0796\times - 0.004x^2$	160.05	<0.0001
	20	$y = - -0.387 + 0.164\times - 0.0066x^2$	187.51	<0.0001
	25	$y = -0.529 + 0.243\times - 0.004x^2 - 0.000077x^3 + 0.0000033x^4 - 0.000000037x^5 - 0.0000000001x^6$	775.92	<0.0001
Female	15	$y = - -0.155 + 0.102\times - 0.008x^2 + 0.000296x^3 - 0.0000052x^4 + 0.000000043x^5 - 0.0000000001x^6$	192.09	<0.0001
	20	$y = - -0.595 + 0.340\times - 0.019x^2 + 0.000533x^3 - 0.0000079x^4 + 0.000000058x^5 - 0.0000000002x^6$	271.60	<0.0001
	25	$y = - -0.553 + 0.267\times - 0.0097x^2 + 0.000158x^3$	367.13	<0.0001

stant temperature (Table 1). The observed cumulative temporal differences in mobility by gender at each temperature are shown in Fig. 2.

Effect of Length of Time in Cold Storage on Adult Locomotor Activity. The locomotor activity of mass-reared codling moths was significantly influenced by an interaction between length of time in cold storage (0, 24, 48, or 72 h) and rearing strategy (D or N) ($F = 2.82$; df = 3, 254; $P = 0.0397$) (Fig. 3). However, we found no significant influence of insect gender under this experimental protocol. When diapaused adults were stored at 2°C for 24, 48, and 72 h, they were significantly less mobile than were diapaused adults that did not experience cold storage (0 h). In contrast, length of time in cold storage did not significantly influence the mobility of adult codling moths reared through standard production protocols. Furthermore, the type of rearing strategy (D or N) did not significantly influence adult mobility when comparisons were made at each storage time. Even though the mean ± SD mobility count (1,024.9 ± 1149) for diapaused adults at 0 h of cold storage was almost twice as high as the mobility count (579.1 ± 594) for non-diapaused (standard production) adults at 0-h cold storage, these means were not significantly different. Mobility counts for diapaused adults at 0 h of cold

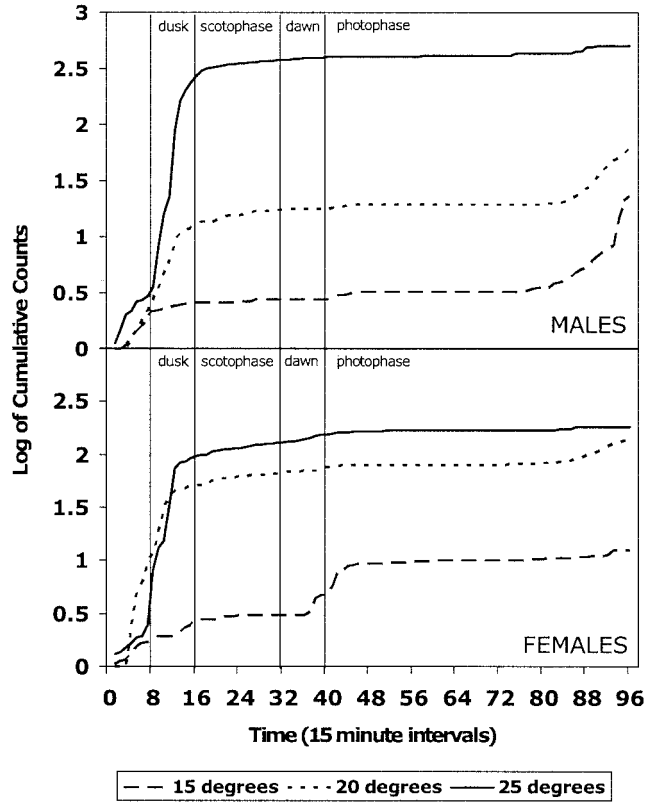

Fig. 2. Observed cumulative mobility counts for 24–48-h-old adult *C. pomonella* tested at three different constant temperatures (15, 20, and 25°C).

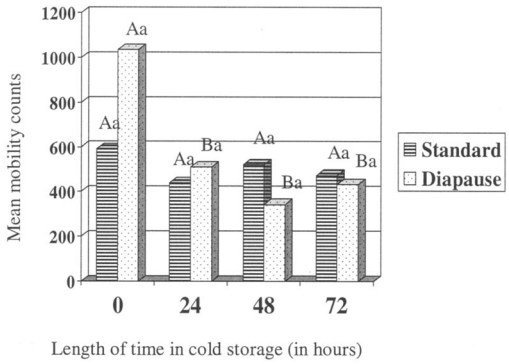

Fig. 3. Effect of length of time in cold storage (2°C) on the locomotor activity of 24–48-h-old diapaused and nondiapaused (standard) adult *C. pomonella* as measured in infrared actographs. Uppercase letters compare means between different storage durations within each rearing strategy. Lowercase letters compare means between diapausing and nondiapausing individuals within individual storage times.

storage were highly variable, with 21.8% of the tested population having counts that exceeded 1,600. In contrast, only 6.1% of the nondiapaused adults at 0-h cold storage had counts that exceeded 1,600.

Discussion

Quality assessment of mass-reared insects should evaluate the conservation of natural behavioral traits that would result in good performance after release in the field (Gandolfi et al. 2003). After undergoing laboratory adaptation, desirable behavioral attributes in mass-reared insects may be compromised by rearing under artificial conditions, such as constant temperature, and by storage conditions and duration before field release (Bloem et al. 1998, Steinberg et al. 1999). As such, our objective was to evaluate the influence of three different constant ambient temperatures (15, 20, and 25°C) and different lengths of adult cold storage (0, 24, 48, or 72 h at 2°C) on the locomotor activity of adult *C. pomonella*, mass-reared through diapause or standard production protocols.

To realize areawide suppression of *C. pomonella*, the OKSIR Program in Canada makes periodic releases of mass-reared and irradiated codling moths into the apple and pear orchards of south central British Columbia for ≈20 wk each year. In general, moth releases begin in early May and continue uninterrupted until mid- to late September. During this time period, ambient field temperatures as well as general environmental conditions may vary widely. Batiste et al. (1973) and Knight et al. (1994) studied the mating-flight response of wild male codling moths by using timing traps. They reported that male flight did not occur when field temperatures were above 26.6–30°C or below 12.7–13°C, respectively, for studies conducted in California and Washington. Bloem et al. (1998) showed that mean weekly dusk temperatures correlated well with weekly trap captures of mass-reared irradiated males in pheromone-baited traps within each season. Subsequently, Bloem et al. (2004) reported that daily recapture of irradiated mass-reared males in pheromone traps showed a more typical pattern in the summer than in the spring, i.e., moths were recaptured in high numbers during the first 3–4 d after release.

Our laboratory data revealed no significant differences in the mobility of unirradiated diapaused and nondiapaused adult *C. pomonella*, which was congruent with the findings of Bloem et al. (2006) when *C. pomonella* were not irradiated. However, not unexpectedly, adult mobility was significantly higher for both males and females at ambient temperatures of 25 and 20°C than at 15°C. In addition, the locomotor activity of males and females was similar at the lower constant temperatures (20 and 15°C); whereas males were found to be significantly more mobile than females at 25°C. This temperature is high enough for virgin females to engage in what would be "normal" activity for unmated females, female calling, which would not translate into higher mobility in this gender. In contrast, normal activity for virgin males would be to disperse as they seek mates. Thus, we would expect to record increased locomotor activity for males at higher temperatures. It seems that the increased locomotor activity for virgin males recorded in our laboratory tests at 25°C may reflect their mating related activity.

Temporal analysis of the data revealed that males exhibited a weak bimodal pattern of locomotor activity at 25°C, with the largest peak occurring at dusk and a small secondary peak registering during photophase at mid-afternoon (≈1500 h; interval 76 in Fig. 2). The time of this second activity peak corresponded to approximately 6 h before dusk on a typical midsummer day in British Columbia. When males were tested at 20°C, the highest activity peak also occurred at dusk; however, some mobility continued into scotophase. As mentioned above, a secondary peak was detected in mid-afternoon. However, the magnitude of the secondary peak was significantly greater at 20°C than at 25°C, accounting for ≈30% of the total activity for males. The shift in diel activity pattern was even more pronounced when males were tested at 15°C. Although some activity occurred during dusk and scotophase, the highest mobility was recorded at mid-afternoon beginning ≈1500 h. The timing of this activity peak at a temperature of 15°C corresponded to the onset of dusk on a typical spring day in British Columbia and represented ≈65% of the total male activity recorded at this temperature. Female activity patterns were similar to those of males except that the secondary activity peak was greatly reduced and began later in the afternoon (≈1700 h; interval 84 in Fig. 2). Interestingly, females tested at 15°C exhibited a strong period of activity during dawn and the beginning of photophase.

The mobility patterns recorded at 25°C are typical and have been observed in wild *C. pomonella* (Batiste et al. 1973, Pitcairn et al. 1990). Batiste et al. (1973) showed that air temperature may cause a shift in peak capture of wild moths in timed traps. In their study,

cool temperatures advanced peak captures 1 to 2 h before sunset. This was confirmed in the laboratory by Castrovillo and Cardé (1979) who reported that a reduction of 7°C 3 h before dusk shifted male and female activity into photophase. Therefore, when codling moths are subjected to cool temperatures, adaptive behaviors allow them to shift their activity to the warmest part of the day to maximize the opportunity for flight, mating, and oviposition. Similar to the behavior in wild *C. pomonella*, we found that laboratory-adapted, mass-reared moths exposed to lower constant temperatures during a long day photoperiod shift their pattern of activity to mid-afternoon to take advantage of the time of day at which temperatures would typically be the highest.

The patterns of activity we observed when males and females were tested at 25°C were similar to those reported for 2-d-old moths tested by Keil et al. (2001a) at 22°C. However, our data showed a small secondary period of activity taking place during photophase at mid-afternoon (1500 h for males and 1700 h for females). In addition, moths tested in Keil et al. (2001a) were overall less mobile than those tested herein. This variation in mobility may be influenced by differences in the genetic stock and in the degree of laboratory adaptation between the two colonies. In fact, Dorn et al. (1999) reported an activity loss in their laboratory-reared colony compared with field-collected populations, and because mobility in codling moth is a heritable trait (Schumacher et al. 1997b, Keil et al. 2001b), laboratory rearing favors the more sedentary genotype (Gu et al. 2006).

When diapaused adults were stored at 2°C for 24, 48, and 72 h, they were significantly less mobile than were diapaused adults that did not experience cold storage (0 h). This difference in mobility was especially influenced by the inability of diapaused adults undergoing cold storage to record high mobility counts. Highly mobile adults (those with mobility counts above 1,600) represented a relatively large proportion (21.8%) of the population when diapaused adults did not experience any cold storage. However, the percentage of adults with mobility counts above 1,600 was reduced to 8.5, 0, and 0% for diapaused adults stored at 2°C for 24, 48, and 72 h, respectively. In contrast, length of cold storage did not influence the mobility of adults reared through standard production. Also, the percentage of standard production adults with mobility counts above 1,600 was less variable (2.8–6.1%) than for diapaused adults. Last, rearing strategy did not significantly affect adult mobility when comparisons were made within each treatment (storage times; Fig. 3). Because SIT programs require storage of mass-reared insects during the processes of collection, distribution and release, the fact that time in cold storage did not decrease the mobility of mass-reared adult *C. pomonella* is an important and positive finding.

The results presented herein suggest that mass-reared and laboratory-adapted *C. pomonella* produced by the OKSIR Program in Canada retain behavioral attributes that are present in their feral counterparts. Moths were able to shift their flight activity in response to lower ambient temperatures, and experienced no decrease in mobility when moths were stored for up to 72 h at 2°C. It has been predicted that codling moths reared through diapause might have an advantage over standard reared moths with respect to their "cold-hardiness," and therefore they would be more tolerant of cold storage, more mobile at lower temperatures, and exhibit different diel activity patterns. However, because we detected no effect or interaction due to rearing strategy, we surmise that responses to low temperatures by shifting diel activity patterns are derived behavioral traits that may be independent of seasonal or generational (brood) effects.

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References Cited

Batiste, W. C., W. H. Olson, and A. Berlowitz. 1973. Codling moth: influence of temperature and daylight intensity of the periodicity of daily flight in the field. J. Econ. Entomol. 66: 883–892.

Bloem, K. A., and S. Bloem. 2000. Sterile insect technique for codling moth eradication in British Columbia, Canada, pp. 207–214. *In* K.-H. Tan [ed.], Area-wide control of fruit flies and other insect pests. Proceedings of FAO/IAEA Symposium, 28 May 1998, Penang, Malaysia. Penerbit Universiti Sains Malaysia, Penang, Malaysia.

Bloem, S., K. A. Bloem, and S. L. Fielding. 1997. Mass-rearing and storing codling moth larvae in diapause: a novel approach to increase production for sterile insect release. J. Entomol. Soc. Br. Columbia 94: 75–81.

Bloem, S., K. A. Bloem, and A. L. Knight. 1998. Assessing the quality of mass-reared codling moths (Lepidoptera: Tortricidae) by using field release-recapture tests. J. Econ. Entomol. 91: 1122–1130.

Bloem, S., K. A. Bloem, and C. O. Calkins. 2000. Incorporation of diapause into codling moth mass-rearing: production advantages and insect quality issues, pp. 329–335. *In* K.-H. Tan [ed.], Area-wide control of fruit flies and other insect pests. Proceedings of the FAO/IAEA Symposium, 2 June 1998, Penang, Malaysia. Penerbit Universiti Sains Malaysia, Penang, Malaysia.

Bloem, S., J. E. Carpenter, K. A. Bloem, L. Tomlin, and S. Taggart. 2004. Effect of rearing strategy and gamma radiation on field competitiveness of mass-reared codling moths (Lepidoptera: Tortricidae). J. Econ. Entomol. 97: 1891–1898.

Bloem, S., J. E. Carpenter, and S. Dorn. 2006. Mobility of mass-reared diapaused and non-diapaused *Cydia pomonella* (Lepidoptera: Tortricidae): effect of mating

status and treatment with gamma radiation. J. Econ. Entomol. 99: 699–706.

Boving, P. A., R. B. Hutt, and R. E. Short. 1978. An aktograph for detecting insect movement. Trans. Am. Soc. Agric. Eng. 21: 176–179.

Brinton, F. E., M. D. Proverbs, and B. E. Carty. 1969. Artificial diet for mass production of the codling moth, *Carpocapsa pomonella* (Lepidoptera: Olethreutidae). Can. Entomol. 101: 577–584.

Calkins, C. O., and T. R. Ashley. 1989. The impact of poor quality of mass-reared Mediterranean fruit flies on the sterile insect technique used for eradication. J. Appl. Entomol. 108: 401–408.

Calkins, C. O., and A. G. Parker. 2005. Sterile insect quality, pp. 269–296. *In* V. A. Dyck, J. Hendrichs, and A. S. Robinson [eds.], Sterile insect technique. Principles and practice in area-wide integrated pest management. Springer, Heidelberg, Germany.

Castrovillo, P. J., and R. T. Cardé. 1979. Environmental regulation of female calling and male pheromone response periodicities in the codling moth (*Laspeyresia pomonella*). J. Insect Physiol. 25: 659–667.

Cayol, J.P.J. Vilardi, E. Rail, and M. T. Vera. 1999. New indices and method to measure the sexual compatibility and mating performance of medfly (Diptera: Tephritidae) laboratory reared strains under field cage conditions. J. Econ. Entomol. 92: 140–145.

Dorn, S., and H. Gu. 1999. Laboratory evaluation of influence of surface residues of azinphos-methyl on adult activity of the codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae). IOBC WPRS Bull. 22: 195–199.

Dorn, S., P. Schumacher, C. Abivardi, and R. Meyhöfer. 1999. Global and regional pest insects and their antagonists in orchards: spatial dynamics. Agric. Ecosyst. Environ. 73: 111–118.

Gandolfi, M., L. Mattiacci, and S. Dorn. 2003. Mechanisms of behavioral alterations of parasitoids reared in artificial systems. J. Chem. Ecol. 29: 1871–1887.

Gu, H., J. Hughes, and S. Dorn. 2006. Trade-offs between mobility and fitness in *Cydia pomonella* L. (Lepidoptera: Tortricidae). Ecol. Entomol. (in press).

Hsiao, H. S. 1978. Circadian activity of *Heliothis zea* at different temperatures studied with an acoustic actograph. Ann. Entomol. Soc. Am. 71: 115–120.

Huettel, M. D. 1976. Monitoring the quality of laboratory reared insects: a biological and behavioral perspective. Environ. Entomol. 5: 807–814.

Hughes, J., and S. Dorn. 2002. Sexual differences in the flight performance of the oriental fruit moth *Cydia molesta.* Entomol. Exp. Appl. 103: 171–182.

Keil, S., H. Gu, and S. Dorn. 2001a. Diel patterns of locomotor activity in *Cydia pomonella:* age and sex related differences and effects of insect hormone mimics. Physiol. Entomol. 26: 306–314.

Keil, S., H. Gu, and S. Dorn. 2001b. Response of *Cydia pomonella* to selection on mobility: laboratory evaluation and field verification. Ecol. Entomol. 26: 495–501.

Knight, A. L., M. Weiss, and T. Weissling. 1994. Diurnal patterns of adult activity of four orchard pests (Lepidoptera: Tortricidae) measured by timing trap and actograph. J. Agric. Entomol. 11: 125–136.

Lance, D. R., T. M. Odell, V. C. Mastro, and C. P. Schwalbe. 1988. Temperature-mediated programming of activity rhythms in male gypsy moths (Lepidoptera: Lymantriidae): implications for the sterile male technique. Environ. Entomol. 17: 649–653.

Lux, S. 1999. Diagnosis of behavior as a tool for quality control of mass reared arthropods, pp. 66–79. *In* F. Bigler [ed.], Proceedings of the 5th Workshop of the IOBC Global Working Group "Quality control of mass reared arthropods," 25–28 March 1991, Wageningen, The Netherlands. International Organization for Biological Control of Noxious Animals and Plants, Zurich, Switzerland.

Pitcairn, M. J., F. G. Zalom, and W. J. Bentley. 1990. Weather factors influencing capture of *Cydia pomonella* (Lepidoptra: Tortricidae) in pheromone traps during overwintering flight in California. Environ. Entomol. 19: 1253–1258.

Proverbs, M. D. 1971. Orchard assessment of radiation-sterilized moths for control of *Laspeyresia pomonella* (L.) in British Columbia, pp. 117–133. *In* IAEA application of induced sterility for control of lepidopterous populations. Vienna, Austria.

SAS Institute. 1989. SAS user's guide. SAS Institute, Cary, NC.

Schumacher, P., A. Weyeneth, D. C. Weber, and S. Dorn. 1997a. Long flights in *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) measured by a flight mill: influence of sex, mating status and age. Physiol. Entomol. 22: 149–160.

Schumacher, P., D. C. Weber, C. Hagger, and S. Dorn. 1997b. Heritability of flight distance for *Cydia pomonella.* Entomol. Exp. Appl. 85: 169–175.

Steinberg, S., D. Gouldman, and L. Kaminski. 1999. The effect of storage conditions on adult longevity, fertility and sex-ratio of the leafminer parasitoid *Diglyphus isaea* (Walker), pp. 95–101. *In* F. Bigler [ed.], Proceedings of the 5th Workshop of the IOBC Global Working Group "Quality control of mass reared arthropods,", 25–28 March 1991, Wageningen, The Netherlands. International Organization for Biological Control of Noxious Animals and Plants, Zurich, Switzerland.

Todd, E. S., A. S. Robinson, C. Caceres, V. Wornoayporn, and A. Islam. 2002. Exposure to ginger root oil enhances mating success of male Mediterranean fruit flies (Diptera: Tephritidae) from a genetic sexing strain. Fla. Entomol. 85: 440–445.

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